A NEW *PACHYTESTA* OVULE FROM IOWA

A Thesis

by

MARY RACHEL MCCARTY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2007

Major Subject: Geology

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Approved by:

Chair of Committee, Anne Raymond
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ABSTRACT

A New *Pachytesta* Ovule From Iowa. (August 2007)

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A new species of the medullosan seed fern genus, *Pachytesta,* is described from specimens discovered in coal balls from Iowa. The specimens used in this study were located in coal balls, which are concretions of ancient permineralized peat. Anatomical study of the new species was made possible through the use of mounted cellulose acetate peels and photomicroscopy. The ovule is approximately 5.0-5.5 cm long and 2.4 -2.8 cm wide at its mid point. The integument contains a sarcotesta with 12 vascular bundles, a sclerotesta of radiating fibers and variable thickness, and an endotesta consisting of a thin cuticle. The primary ribs of the ovule are commissured. Based on the anatomical features studied, *Pachytesta sp. A.* is most similar to Taylor's (1965) *P. olivaeformis, P. composita, P. illinoensis* group and is potentially a member of this group.

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TABLE OF CONTENTS

LIST OF FIGURES

FIGURE Page

CHAPTER I

INTRODUCTION

All coals accumulated in ancient peat swamps (Taylor et al., 1998). Carboniferous wetlands displayed a range of flora; many were distinctly different from plants of later time periods. The dominant plants of Late Carboniferous terrestrial habitats belonged to gymnosperms (cordaites and seed ferns) and lower vascular plants (lycopsids, ferns, sphenopsids). The major producers of biomass preserved in the Late Carboniferous coal record are lycopsids and ferns, followed by sphenopsids, seed ferns, and cordaites (DiMichele and Phillips, 1994; Raymond et. al., 2001).

A great deal of paleobotanical data from the Carboniferous come from permineralized macrofossils found in coal balls. Coal balls, which are concretions of permineralized peat, preserve details of the anatomy of vegetative and reproductive organs, including seeds. This anatomical information can be used to reconstruct the entire body of a plant and place it ecologically. Data from coal balls suggests that the coals created from Late Carboniferous peat represent multiple habitats over time (DiMichele and Phillips, 1994). Late Carboniferous peat-accumulating environments encompassed a wide environmental range from complete land exposure to environments of nearly continuous flooding. Nutrient levels ranged from very low to very high within Late Carboniferous mires (DiMichele and Phillips, 1994).

Coal balls are essentially permineralized peat. They are formed when

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This thesis follows the style of the Review of Palaeobotany and Palynology.

carbonate minerals precipitate from water during or directly after peat accumulation. Typically, the carbonate mineral that precipitates out of water and into the peat is calcite; although some coal balls have a matrix of dolomite or pyrite (Scott et al., 1996). Late Carboniferous coal balls initially were discovered in 1855 (Scott et al., 1996). Although silicified peat has a sporadic stratigraphic distribution from the Early Devonian onward, coal balls (i.e. carbonate or pyritic permineralizations of peat) appear confined to the Late Carboniferous and earliest Permian (Phillips, 1980). The significance of coal balls as a resource for the study of plant evolution and ecology was immediately recognized. However, coal balls also offer valuable insights into the relationship between climate, the formation of peat, and the Paleozoic Carbon cycle (Scott et al, 1996; Raymond et al., 2001).

Coal balls preserve plant fossils in all stages of decomposition, from unrecognizable plant debris to seeds having pollen with pollen tubes, preserved during the process of fertilization (Rothwell and Taylor, 1982). The plant fossils in coal balls also show a range of developmental states. The challenge for systematic studies based on coal-ball fossils is to separate differences due to taphonomy and developmental stage from taxonomic differences.

CHAPTER II

A NEW *PACHYTESTA* OVULE FROM IOWA

1. Introduction

1.1 Medullosan seeds and ovules in the Late Carboniferous permineralized peats

Seeds and ovules are valuable tools in understanding and investigating plant systematics because their anatomy and morphology is often diagnostic at the species level, unlike the anatomy and morphology of vegetative organs. In this study, I investigate a permineralized ovule (unfertilized seed) from a Late Carboniferous coal of Iowa. The separation of the integument and nucellus place this ovule within the medullosan seed ferns. Its large size, trigonal symmetry and the presence of discrete vascular bundles in the nucellus suggest that it belongs to the genus *Pachytesta.* The medullosan seed ferns flourished in Late Carboniferous wetlands, although relatively little is known of their reproductive ecology.

Seeds and ovules are distinguished by their fertilization status: seeds are fertilized, and ovules are not. The fertilization of angiosperms occurs early in seed development, so most recognizable angiosperm seeds are indeed seeds. However, ancient gymnosperms (cycads, conifers, and gnetaleans) apparently had a wide range of times of fertilization and approaches to seed development. In a few modern cycads, all ovules develop fully, whether or not they are ever fertilized. However, in most modern gymnosperms, unfertilized ovules never develop fully (Norstag and Nichols, 1997). Enigmatically, most permineralized

Carboniferous ‘seeds’ appear unfertilized (Chaloner and Pettitt, 1987). There are a number of possible explanations for this. One is that these apparently fully developed seeds are indeed ovules that matured completely without being fertilized. Another explanation is that these were pollinated but not yet fertilized (Chaloner and Pettitt, 1987). Pant and Basu (1973) suggested that fossil ovules/seeds lacking visible embryos could be fertilized seeds with delayed maturation. Finally, many large permineralized seeds, including most medullosan seeds, were broken and distorted, before or during the process of permineralization and it is difficult to see whether or not they were fertilized. Because the fertilization status of my study specimens remains unknown, I refer to them as ovules rather than as seeds.

Brongniart (1874) first assigned ovules from the Stephanian (Kasimovian and Gzhelian stages of the Pennsylvanian) of France to the genus *Pachytesta*. The species identified were *P. incrassata* and *P. gigantea*. Both species were also illustrated in Brongniart’s posthumous publication (1881), and Renault (1896) subsequently provided a more detailed description of this genus.

Hoskins and Cross (1946a) reviewed the species of *Pachytesta* known at that time and demonstrated that the compression-impression seed/ovule genus *Trigonocarpus* is a different preservational state of *Pachytesta.*

Hoskins and Cross (1946b) described a new species of *Pachytesta* from the Atlas Coal (Desmoinean Series) of Iowa, *P. vera*. To date, *P. vera* is the only species of *Pachytesta* to be described based on material from Iowa. Painstaking study of this ovule revealed shrinkage of the endotesta, nucellus, and

megaspore, which is common to many permineralized *Pachytesta* ovules and was also observed in P. *gigantea* by Smoot and Taylor (1983).

Taylor (1965) completed a monograph on the genus *Pachytesta*, including two new species, (*P. saharasperma* and *P. hoskinsii*). In addition he used new examples of six existing species to develop more accurate descriptions. Finally, he removed one previously described species of *Pachytesta* (*P. ovale*) from the genus. Taylor (1965) used the orientation of sclerotesta fibers to propose four groups of *Pachytesta*, which he placed in a phylogenetic sequence. First, he grouped *P. shorensis, P. olivaeformis, P. vera, P. hoskinsi,* and *P. saharasperma, a*ll of which possess layers of interweaving fibers in the sclerotesta. The species *Pachytesta muncii*, subsequently described by Cichan and Taylor (1981), appears to be the sister taxon of *P. vera* and belongs in this group. The trait which characterizes this group, occurs in the earliest known *Pachytesta* (*P. shorensis* and *P. olivaeformis*) (Taylor, 1965), and may be primitive. His second proposed group consists of *P*. *noei*, *P. gigantea*, and *P. incrassata*. These three taxa possess a very thick sclerotesta with embedded vascular bundles. Third, Taylor grouped *P. illinoensis* and *P. composita,* due to their large number of ribs. Finally, he placed *P. stewartii, P. hexangulata,*and *P. pusilla* in a group, because they share a two-part sclerotesta, consisting of an inner longitudinal fiber layer, and an outer radial palisade layer. *Pachytesta berryvillensis*, described by Taylor and Eggert (1969) also belongs in this group.

1.2 Ecology of the Medullosans

Pteridosperms or seed ferns were the dominant group of gymnosperms within the lowlands of the Late Carboniferous; and among the lowland pteridosperms, medullosans were the most widespread. With the exception of a few coals from the Carboniferous of Iowa, medullosans usually represented a relatively minor component of the peat swamp flora. They were, however, the most diverse and abundant plant group growing on siliciclastic soils in the lowlands of the Late Carboniferous (DiMichele and Phillips, 1994).

Medullosan trees were robust, and architecturally complex; producing tops with numerous leaves that stayed attached to the stem (Dimichele and Phillips, 1994). Medullosans had very little wood and thus contributed only a small amount of woody debris to coal beds (DiMichelle and Phillips, 1994). They had high resin content and produced the biggest seeds known from the Late Paleozoic, some of which were up to11 cm in length (Taylor, 1965). The seeds likely did not disperse easily due to their large size. This suggests medullosans were heavily dependent upon sexual reproduction to maintain the genetic diversity of the population (DiMichelle and Phillips, 1994).

Medullosan communities often grew at the edge of peat-accumulating swamps and have more and larger invertebrate coprolites than cordaite-dominated communities (DiMichelle and Phillips, 1994, Raymond et. al 2001). These observations, along with the diversity and abundance of medullosans in lowland communities growing on siliciclastic soils, suggests that medullosans

probably required higher nutrient conditions than other peat-accumulating swamp communities (DiMichelle and Phillips, 1994, Raymond et. al 2001).

Although medullosans generally contributed less than 25% to peat-accumulating communities (Phillips et al., 1985), some of the cordaitean-dominated coals of Iowa contain a diverse and abundant medullosan assemblage. For example, medullosans are the most common taxon in 44% of the coal balls (permineralized peat concretions) from the Williamson No. 3 Mine deposit in Iowa (Raymond et. al, 2001). Three medullosan foliage genera occur in the cordaitean-dominated coals of Iowa: *Neuropteris*, *Alethopteris*, and *Reticulopteris*. Medullosan ovules from these deposits include an undescribed species of *Stephanospermum*, as well as all four of Taylor's (1965) *Pachytesta* groups: *P. vera* (group 1); *P. noei*, (group 2), *P. composita*, (group 3) and additional undescribed species, one of which belongs to the *P. stewartii-P.hexangulata-P.pusila-P.berryvillensis* group of Taylor (1965).

The medullosan flora of these Iowa coals provides a unique opportunity to extend our knowledge of medullosan ovules and reproductive biology, as well as improve what we know about the development of modern cycads. In this paper, I describe a new species of *Pachytesta* from the Shuler Mine in Dallas Co., Iowa*. P. sp. A,* based on ten specimens that vary in completeness. *P. sp. A*. is most similar to *P. illinoensis* and belongs within the *composita-illinoensis* group of Taylor (1965).

2. Materials and Methods

2.1 Locality and Biostratigraphic Framework

Brotzman (1974) separated the Iowa coals that contain coal balls into two groups (Fig. 1). The lycopsid-dominated Lovilia deposit, and perhaps the Tillotson deposit described by Darrah (1941), belong to the younger group. The cordaitean ovules, *Cardiocarpus spinatus var. corpulentius* and *C. oviformis* characterize the Lovilia deposit (Brotzman, 1974). Medullosan ovules from the Lovilia deposit include *P. noei* and *P. stewartii* (Klare, 1987). Based on macrofloral remains, Brotzman (1974) correlated the Lovilia deposit to the Bevier Coal of Kansas and the Houchin Creek (Sumum) No. 4 Coal of Illinois. Peppers (1996) placed these coals in the middle Desmoinesian or Westphalian D (ICS Moscovian) (Fig. 1).

Most Iowa coals that have coal balls, including the Shuler, Urbandale, Williamson #3, and Star deposits, belong to Brotzman's older group, referred to here as the diverse cordaitean coals. Cordaitean gymnosperms generally predominate in these deposits, which contain the following cordaitean ovules: *Nucellangium glabrum*, *Mitrospermum florin , M. leeanum, Cardiocarpus spinatus var macilentus,* and *C. magnicellularis* (Brotzman, 1974; Costanza, 2003; Raymond, 1988; Raymond and Phillips, 1983). Based on specimens in the Harvard Botanical Museum and published reports, the medullosan ovules found in these deposits include: *Pachytesta sp. A nov. sp., P. vera, P. composita*, *P. noei, Stephanospermum sp.*, and additional undescribed species (Hoskins and Cross, 1946a, Taylor, 1965).

Conodont biostratigraphy and palynostratigraphy indicate a latest Atokan through earliest Desmoinesian age for the diverse cordaitean coals (Lambert, 1992; Ravn, 1986). In Iowa, this interval includes the latest Atokan Blackoak coal, the earliest Desmoinesian Cliffland coal (Ravn et al., 1984). Based on field relationships and mining records, the coal mined at the Urbandale Mine and the nearby Shuler Mine was probably the earliest Desmoinesian Cliffland coal (Howes et al., 1989).

2.2 Specimens and Sample Preparation

The material used in this study was collected from the Shuler and Urbandale mines near Des Moines, Iowa in the 1930's and 1940's by F. O. Thompson, who donated the material to Harvard University. Three coal balls (two from the Shuler, and one from the Urbandale) contained specimens of the new *Pachytesta*, which has a unique ribbed sclerotesta. One of the Shuler coal balls (H.U. 64982) has a pyritic matrix and contains two of the new *Pachytesta* ovules. This coal ball was cut and peeled at Harvard University using the parlodion peel method in the 1930's or 1940's. The counterpart is not available and has probably disintegrated; however a parlodion peel of the counterpart is available for study. The second Shuler coal ball (H.U. 64984) has a calcite matrix and contains an oblique cross section of the new ovule. This coal ball was cut by F.O. Thompson and sent to Harvard in 1936. The counter part of this coal ball was not found in the crate. The Urbandale coal ball (H.U. 64899) was used in a study of the paleoecology of the Urbandale Mine (Raymond and Phillips,

1983) and has since disintegrated. However, 12 cellulose acetate peels made from this coal ball, containing six specimens and one fragment of the new *Pachytesta* ovule, are available for study. Two peels from this coal ball contain nearly perfect transverse sections through the middle and apex of one ovule (ovule D). Another peel reveals a second ovule (ovule E) in nearly perfect longitudinal section. Although the original coal ball that the peels were taken from is unavailable for further study, the ovules in the existing peels reveal aspects of the vascular system and micropyle not seen in the Shuler specimens. An additional specimen from the Shuler Mine (H.U. 64983, ovule C), consisting of the ovule cavity and small fragments of attached sclerotesta, comes from the Paleobotanical Teaching Collection of Harvard University. Collectively, ten ovules of the proposed species are available for study as peels or as specimens in coal-balls (Table 1). All peels, mounted slides, and remaining coal ball material are currently housed in the Paleobotanical Collection of Harvard University.

The pyritic coal ball from the Shuler Mine (H.U. 64982) was cut strategically to obtain cross sections of ovule A at the base, mid section, and apex, and to obtain a longitudinal section of the middle and apex of ovule B. Ovule B was exposed on the original cut surface of the coal ball and the base of this ovule is in the missing counterpart. All cuts were made using an Isomet ^{Tm} saw, manufactured by Beuhler Ltd., Evanston IL 60204.

Coal balls from Iowa contain a high concentration of finely disseminated pyrite in the matrix, making them prone to cracking and dissolution. To prevent

damage to the specimens, we impregnated newly exposed surfaces with thin, non-viscous epoxy after each saw cut (Epotec 301, manufactured by Epoxy Technology, Inc., Billerica, Massachusetts 01821). This epoxy infiltrates small cracks and tiny void spaces in the surface of the coal ball and protects the coal ball from disintegration during repeated etching.

Cellulose acetate peels were used to reveal the cellular anatomy of specimens, following the technique outlined in Joy et al., (1956). We mounted peels on glass slides using Canadian balsam. After slide preparation, we documented the morphology and anatomy of the new ovule using the Zeiss Axioplan 2 reflected and transmitted light materials microscope with an attached AxioCam HRc digital camera, and the Leica MZ75 stereo-microscope with an attached Spot Insight color digital camera, manufactured by Diagnostic Instruments, Inc.

3. Directory of Specimens

Pachytesta sp. A.

Ovule A – peels and slides and permineralized specimen in coal ball HU 64982 Shuler Mine, Dallas Co., Iowa (Paleobotanical Collection, Harvard University)

Ovule B- peels and slides and permineralized specimen in coal ball HU 64982, Shuler Mine, Dallas, Co., Iowa (Paleobotanical Collection, Harvard University)

Ovule C- peels and slides and permineralized specimen in HU 64983, Shuler Mine, Dallas Co., Iowa (Paleobotanical Collection, Harvard University)

Ovule D- slides and peels of HU 64899, Urbandale Mine, Polk Co., Iowa (Paleobotanical Collection, Harvard University)

Ovule E – slides and peels of HU 64899, Urbandale Mine, Polk Co., Iowa (Paleobotanical Collection, Harvard University)

Ovule F – slides and peels and part of coal ball HU64984, Shuler Mine, Dallas Co., Iowa (Paleobotanical Collection, Harvard University)

4. Systematics

Order: Medullosales

Family: Medullosacceae

Genus: *Pachytesta* Bronginart 1874 (Hoskins and Cross emend. 1946b)

Pachytesta sp. A, sp. nov. (Figs. 2 - 17)

Holotype: Ovule A

Paratypes: Ovules B, C, D, E, and F

Repository: The type material currently resides in the Paleobotanical collection, Texas A&M University, College Station, Texas.

Type Locality: Holotype and Paratype Ovules B, C, and F: Shuler Mine, Dallas Co., Iowa, USA; Paraty;pe Ovules D, and E: Urbandale Mine, Dallas Co. Iowa

Type Stratum: Holotype and Paratypes: coal mined at the Shuler and Urbandale Mines, probably the Cliffland coal

Latest Atokan - earliest Desmoinesian, Pennsylvanian, The Atokan and Desmoinesian stages of North America comprise the ICS Moscovian Stage.

Diagnosis: Large, ellipsoidal ovules, 5.0-5.5 cm long and 2.4 – 2.8 cm in diameter. Integument is three-parted. Outer sarcotesta of randomly oriented parenchyma cells. Middle sclerotesta consists of two layers: an exterior layer of interweaving sclerenchyma fibers that form low ridges; and an inner layer composed primarily of longitudinal fibers, with rare fibers wrapping around the

seed in a tangential direction. Inner endotesta is a thin cuticle. Integument has three commissured ribs, which are most visible at the apex, and reduce in prominence towards the base. Nucellus is thin, increasing in thickness toward the apex, with a cuticle facing the endotesta. Micropyle is triangular in cross section and flared at the tip. Pollen chamber is present at apex. Nucellus with discrete vascular bundles, number of nucellar bundles unknown. Estimated number of vascular bundles in sarcotesta is 12. Exterior surface of the ovule nearing the apex is lobed, while the middle exterior and base are smooth.

5. Description

Pachytesta sp. A. is an ellipsoid ovule with trigonal radial symmetry, it is approximately 5.0-5.5 cm long and ranges in width from 2.4-2.8 cm (Fig. 2, and Fig. 3).

Table 1. Diameter of *Pachytesta sp A*

Ovule (Source)	Diameter	Estimated Length	Notes
Ovule A (HU 64982; Shuler Mine)	2.1 cm	5.0 cm	sarcotesta eroded
Ovule B (HU 64982; Shuler Mine)	2.2 cm		perpendicular longitudinal section[a], sarcotesta eroded
Ovule D (HU 64899; Urbandale Mine)	2.8 cm		cross section, sarcotesta eroded
Ovule E (HU64899; Urbandale Mine)	2.5 cm	5.5 cm	longitudinal section, sarcotesta eroded
Ovule 12-1 (HU 64899; Urbandale Mine)	2.2 cm		oblique cross section, sarcotesta eroded
Ovule 12-6 (HU 64889; Urbandale Mine)	unknown		

[a] showing micropyle
[b] perpendicular to the longitudinal axis of the ovule

5.1 Integument

P. sp A has a three-parted integument consisting of an outer sarcotesta, middle sclerotesta and inner endotesta (Fig. 3, Fig. 4).

Sarcotesta

The outer surface of the ovule is relatively smooth, but possesses three slight angulations which indicate the presence of the three primary commissured ribs (Fig. 3, Fig. 4). The outer portion of the sarcotesta may be lacunate.. In general, the cells of the sarcotesta have thin walls (Fig. 5). The sarcotesta possesses no resin-filled secretory cells or canals. However, a few cells in the sarcotesta, which appear associated with the vascular bundles and primary ribs, have somewhat thicker, dark, walls (Fig. 6). These will be referred to as “dark walled cells” throughout this text.

Most of the sarcotestal cells are tabular or radially elongate (as opposed to isodiametric), with their longest dimension perpendicular to the long axis of the ovule (Fig. 5, Fig. 7). Inner sarcotesta cells vary in orientation depending on the orientation of cells in the adjacent sclerotesta. The cells of the sarcotesta align horizontally and tangentially at the “top” of the sclerotestal crenulation (Fig. 7). The cells located between the crenulations of the sclerotesta have a radial orientation, and are ellipsoidal in cross section.

The sarcotesta of all *P. sp. A* ovules is eroded, particularly in the mid section. The thickness of the preserved sarcotesta ranges from 4.5 mm at the base of the ovule to 0.5 mm in the middle of the ovule to 4.5 mm at the apex. The thickness of the sarcotesta decreases slightly at the primary and secondary ribs; largely because the sclerotesta thickens at these locations. It thins more significantly at the primary rib locations, while thinning only slightly at the secondary ribs (Fig. 3). The sarcotesta tapers to a point at the base of the ovule (Fig. 2) and the base of the pedestal is exposed at the exterior of the ovule. Areas of crushed cells at the edge of the sarcotesta, which are sometimes associated with vague radial arrays of dark walled cells, appear to indicate the original position of the vascular bundles (Fig. 6, Fig. 8).

Sclerotesta

The sclerotesta has three primary ribs. The sclerotesta is often cracked at the primary ribs of the ovule. These cracks appear to coincide with the primary commissures and may be caused by weakness of the ovule tissue associated with the commisured ribs (Fig. 9). The primary ribs expressed in the sclerotesta are 2-3 mm wide in the middle of the seed. No trabeculae are associated with the primary ribs of the sclerotesta. Secondary ribs in the lower two thirds of the seed are expressed as slight angulations of the sclerotesta. Near the apex, the sclerotesta thickens in the vicinity of the secondary ribs, which are expressed as broad triangular features in cross section (Fig. 4).

The inner layer of the sclerotesta consists predominantly of longitudinally

oriented fibers. Occasionally fibers in this layer wrap around the ovule in a horizontal, tangential orientation (Fig. 10). The middle portion of the sclerotesta consists of brown to black fibrous cells, which form 20-23 ridges between each pair of primary ribs in the middle of the ovule (Fig. 3, Fig. 7, Fig. 11).

The sclerotesta may possess two different types of secretory cells. In ovule C, which is especially well preserved, large ovoid cells, which could be secretory in function, intermingle with the fibers of the sclerotesta (Figure 11). Ovule C appears unique in having excellent cellular preservation of the outer layer of the sclerotesta. In most ovules, the outer portion of the sclerostesta is black and appears amorphic, perhaps due the presence of resin filling the fibers. The source of this resin could have been the ovoid secretory cells of the middle sclerotesta or the radiating fibers that form the crenulations or ridges.

Because of the crenulations or ridges, the sclerotesta undulates in thickness from 0.5 to 2 mm thick at the middle of the ovule. Measured across the crenulations, the sclercotesta ranges from 3 mm thick at the base to 1 mm thick at the middle, to 0.5 mm thick at the apex of the ovule (Fig. 2, Fig. 3, Fig. 11). The thickness of the sclerotesta in cross section increases approaching the primary ribs. However, it does not thicken at the location of the secondary ribs in the lower two thirds of the ovule. Near the apex, the sclerotesta thickens in the vicinity of the secondary ribs (Fig. 12, Fig. 13).

Endotesta

The endotesta is a thin, black, cuticle located along the exterior edge of the nucellus (Fig. 14). It is approximately 1-2 microns thick in cross section, at the mid point of the ovule. The endotesta, which can be recognized by the fragmentary cell walls facing toward the sclerotesta, appears to remain the same thickness throughout the length of the ovule. When present, the endotesta is often pulled away from the sclerotesta (Fig. 14). Hoskins and Cross (1946b) and Smoot and Taylor (1983) described a similar taphonomic condition in *P. vera* and *P. gigantea*.

5.2 Apex

Reconstructions of the ovule apex in cross section based on the most complete specimen showing the ovule apex (Fig. 15) reveal that the apex of the ovule is a blunt equilateral triangle formed from lobes of sarcotesta, which is 5-9 mm on each side. These large, lobes constrict the apical opening, to a triradiate star (Fig. 15, Fig. 16). The sclerotesta forms a narrow neck, 2 mm in diameter, and 9 mm high at the top of the seed cavity. It is this narrow neck that is constricted by the sarcotesa lobes. The micropyle, which is triangular in cross section and flared at the tip, is formed from an extension of the endotesta. In ovule B, the micropyle has drawn back from the inner surface of the sclerotesta after death. In life, the micropyle probably extended to the top of the ovule in the center of the opening (Fig. 13, Fig. 15). In ovule B, the approximate distance between the base of the micropyle and the base of the ovule cavity is the same

as the approximate distance between the flared tip of the micropyle and the top of the sarcotestal lobe (Fig. 13).

Below the sclerotestal neck, the micropyle connects to the pollen chamber. Although broken, this chamber appears to have a multicellular 'floor' (Fig. 13). There is a single pollen grain present in the corner of the triangular micropyle in the ovule F cross section from Urbandale; but this pollen is *Florinites sp.*, which belongs to the cordaitean gymnosperms (Fig. 16).

5.3 Nucellus and Chalazal

The megaspore of the ovule is now a flattened envelope that has collapsed from its original ellipsoidal shape. The nucellus is preserved with its cuticle, which faces the endotesta (Fig. 14). It ranges from 2 to 5 mm in thickness; thickening toward the micropyle and thinning toward the chalazal in longitudinal section. The nucellus joins the pedestal at the base of the ovule (Fig. 2). The pedestal is fibrous and slightly attenuated, increasing in width towards the interior of the ovule (Fig. 2). On the undistorted side of the pedestal, there is a prominent break between the pedestal and the nucellus and a small chalazal skirt below (Fig. 2). The nucellus forms internal ribs at the primary rib locations of the ovule.

5.4 Vascular system

Medullosan ovules have a separate vascular system for the nucellus and the integument. In *Pachytesta*, the nucellar vascular system consists of discrete

vascular bundles. A few discrete vascular strands are preserved in the nucellus of ovule B (Fig. 14), which is consistent with the identification of this ovule as a species of *Pachytesta*.

In *P. sp. A*., the vascular system of the integument apparently lay very close to the exterior of the sarcotesta and is seldom preserved. In the apical cross section of ovule A, areas of distorted cells at the edge probably indicate the position of the missing vascular bundles (Fig. 12). In ovule D, clusters of dark walled cells at the edge of sarcotesta probably indicate the location of the vascular bundle (Fig. 6, Fig. 8). In a cross section through the middle of ovule D, four clusters of dark walled cells occur between each primary rib, suggesting a total of 12 vascular bundles in the integument.

6. Discussion

Pachytesta sp. A. is placed in the order Medullosales, based on its radial symmetry and the separation of the integument (the sarcotesta, sclerotesta and endotesta) from the nucellus. Separation of the integument from the nucellus distinguishes medullosans from lyginopterid ovules. In *P. sp. A.*, as in *P. gigantea* (Smoot and Taylor, 1983), the cuticle associated with the nucellus lies next to the cuticle associated with the endotesta, indicating the separation between these two parts of the ovule (Fig. 14). An idealized drawing of *P. sp. A.* in longitudinal section and apical cross section has been included for anatomical reference (Fig. 17).

The ovule is placed in the genus *Pachytesta* based on its trigonal symmetry, three commissured ribs, and the presence of vascular bundles in the nucellus. The nucellar tracheids of the other well-characterized medullosan ovule genus, *Stephanospermum*, form a tracheal net rather than discrete vascular bundles. Based on the presence of tangential, horizontal fibers in the innermost sclerotesta, a ribbed sclerotesta and a unique apical configuration, *P. sp. A* has been placed in a new species.

Pachytesta Sp. A can be readily distinguished from all other *Pachytesta* species due to the presence of abundant short ridges in the sclerotesta, between the three primary ribs. These short ridges, which are 2-3 mm tall, are formed by interweaving bands of fibers in the middle layer of the sclerotesta. In cross section, these arrays give the sclerotesta of *P. sp. A* a crenulated look. Four other species of *Pachytesta* have abundant ribs or ridges on the sclerotesta. *P. olivaeformis* has nine short tertiary ribs which result from regular variations in the length of straight radial fibers (Taylor, 1965: Plate 22, Fig 137). In both *P. composita* and *P. illinoensis,* the sclerotesta ribs are quite tall. In *P. composita* these are formed from tangential horizontal fibers; in *P. illinoensis*, these are formed from straight radial fibers. In *P. berryvillensis*, the ribs occur on the inner side of the sclerotesta and extend into the seed cavity (Taylor and Eggert, 1969).

Although less readily apparent, *P. sp. A* also differs from all described species of *Pachytesta* in the orientation of the innermost fibers of the sclerotesta. In all previously described species of *Pachytesta*, the inner layer of fibers in the sclerotesta has a longitudinal orientation, parallel to the long axis of the ovule (*P.*

olivaeformis, P. muncii, P. noei, P. gigantea, P. composita, P. illinoensis, P. stewartii, P. pusilla), or a slightly oblique-longitudinal orientation (*P. shorensis, P. vera, P. saharasperma, P. hexangulata*) (Taylor, 1965). In *P. sp. A,* the innermost fibers of the sclerotesta occasionally have a horizontal, tangential orientation, wrapping around the ovule perpendicular to the long axis (Fig 10, Fig. 11).

Finally, *P. sp. A*. has a unique apical configuration in which the sclerotesta forms a neck that is triangular in cross section and 5 mm long (Fig. 12, Fig. 13). At the apex of the ovule, six lobes of the sarcotesta (one for each primary and secondary lobe), formed a triradiate star-shaped opening above the sclerotesta neck (Fig 15). The micropyle, which is triangular in cross section and has a flared tip, is formed from endotesta and probably extended to the apex of the seed in the middle of the triradiate star-shaped opening. It is not clear whether parenchyma filled the sclerotesta neck of *P. sp. A*.

Unlike *P. sp. A*, most other *Pachytesta* have a simple apical configuration, with a micropyle composed of endotesta and sclerotesta. The apical configuration of *P. illinoensis* is the most similar to *P. sp. A.* In *P. illinoensis*, the micropyle is formed from endotesta and is surrounded by a collar formed from the sclerotesta and sarcotesta of the primary, secondary and tertiary ribs. However, in *P. illinoensis*, the collar is wider than the sclerotesta neck of *P. sp. A*. Also, in *P. illinoensis*, the sarcotesta does not constrict the opening of the collar at the seed apex as in *P.sp. A* (Taylor, 1965). In *P. illinoensis*, the endotesta of the micropyle was surrounded by a cone of parenchyma lined with secretory

cells, whereas in *P. sp. A* it is not clear whether the endotesta of the micropyle was surrounded by parenchyma.

Taylor (1965) used the orientation of sclerenchyma fibers in the sclerotesta to distinquish *Pachytesta* lineages. Superficially*, P. sp. A*. is quite distinct and does not obviously fit into any of Taylor's *Pachytesta* lineages. However, based on the abundance of ribs, the orientation of fibers in the sclerotesta, and the apical configuration, *P. sp. A*. appears to belong in Taylor's *P. composita - P. illinoensis* group, hereafter referred to as the *composita-illinoensis* group. *P. olivaeformis*, with nine tertiary ribs, may belong in this group as well. If so, all of the ovules in this group have nine or more ribs or ridges in addition to their primary ribs. In the middle of the seed, *P. sp. A*. has three primary, three secondary and 18-20 'tertiary' ridges, although secondary ribs and 'tertiary' ridges are difficult to distinguish. Scott et al. (1996) described *P. olivaeformis* as having nine tertiary and no secondary ribs for a total of 12 ribs. *P. composita* has as many as 21 secondary and tertiary ribs; *P. illinoensis* can have as many as 42 (Taylor, 1965).

Species within the *composita-illinoensis* group also share apical characters with *P. sp. A*. Like *P. sp. A.*, both *P. composita* and *P. illinoensis* have micropyles with a triangular cross section. As discussed above, both *P. illinoensis* and *P. sp. A* have a micropyle composed of endotesta surrounded by a collar or neck of sclerotesta and sarcotesta (Taylor, 1965).

Despite all of the similarities between *P. sp. A.* and the *P. olivaeformis* lineage, the ovule has some distinctly different traits as well. *P. sp. A.* lacks

secretory canals in the sarcotesta, while members of Taylor's *composita-illinoensis* group have these. Additionally, both *P. composita* and *P. illinoensis* have many more vascular bundles in the integument than *P. sp. A*. However, like *P. sp. A, P. olivaeformis* has relatively few vascular bundles (estimated 8-12) vascular bundles in the integument (Taylor, 1965).

P. sp. A shares a number of characters with *P. stewartii*: lack of doubled vascular bundles at the primary ribs, vascular bundles between, and not adjacent to primary ribs, lack of secretory cells and canals in the integument and nucellus, possession of a pollen chamber floor and lack of a pollen drop mechanism associated with the micropyle. The vascular characters on this list are primitive for *Pachytesta*. It is not clear whether the pollen chamber floor and the pollen drop mechanism are primitive or are derived characters with respect to *Pachytesta* (Serbert and Rothwell, 1995). The presence of a pollen chamber floor may relate to the developmental stage of the ovule at the time of permineralization; pollen drop mechanisms are rarely preserved. The lack of secretory cells and canals in the sarcotesta and nucellus is probably a derived trait. However, this trait may have arisen in *P. sp. A* and *P. stewartii* independently. *P. sp. A.* lacks the derived trait that pulls Taylor's *P. stewartii - P. hexangulata – P. pusilla* group together, which is the presence of a radial palisade layer on the exterior of the sclerotesta. *P. sp. A* does not appear to be closely related to this group.

Like species in Taylor's *P. vera – P. Saharasperma – P. hoskinsii* group, which probably includes *P. muncii, P. sp. A*. has a sclerotesta composed in part

of interweaving bands of fibers. However, this appears to be a primitive condition for *Pachytesta*. The *P. vera – P. Saharasperma – P. hoskinsii* group shares none of the derived characters of *P. sp. A*, including its multi-ridged sclerotesta, the presence of horizontal, tangential fibers in the innermost layer of the sclerotesta, and its elaborate apical configuration.

Taylor's *P. noei – P. gigantea – P. incrassata* group shares a number of derived characters, including doubled vascular bundles within the integument at the primary ribs, vascular bundles in the sclerotesta, and an extremely thick sclerotesta. *P. sp. A*. lacks any of these derived characters.

Seed characters suggest that the sister group of the medullosan seed ferns may be modern cycads (Fig. 18). Cycads and medullosans share the following derived characters: radially symmetric seeds borne on leaves, a separate vascular system for the nucellus and integument, and separation of the nucellus from the integument. In modern cycads, seeds of a few species develop fully whether or not they are pollinated (Norstag and Nichols, 1997); this may have been the case for all medullosan ovules (Stewart, 1951).

Cycads differ from medullosans in having seeds borne of leaves organized into apical cones (Norstag and Nichols, 1997). In cycad seeds, the integument and nucelllus are fused in the lower one half to two thirds of the seed (Chamberlain, 1906). Cycads have hausitorial pollen, in which pollen tubes grow into the nucellus of the ovule (Norstag and Nichols, 1997). These tubes facilitate transfer of nutrients from the mother plant to the male gametophyte. Fertilization

is accomplished by swimming sperm released into the pollen tube. Medullosans probably did not have hausitorial pollen (Chaloner and Petitt, 1987).

The two best characterized genera of medullosan seed ferns, *Pachytesta* and *Stephanospermum*, are characterized by three commissured ribs. Otherwise *Stephanospermum* has hexagonal symmetry and a tracheal net rather than discrete vascular bundles in the nucellus (Serbert and Rothwell, 1995). In addition, at least one species of *Stephanospermum* was borne upright on slender branches (Drinnan et al., 1990), which may have been highly modifed leaves. *Pachytesta* is distinguished from *Stephanospermum* by having three primary ribs and three or more subordinate ribs, which are not as strongly expressed as the commissured primary ribs (Hoskins and Cross, 1946b, Taylor, 1965).

The stratigraphic range of both *Pachytesta* and *Stephanospermum* is Atokan through Missourian (Moscovian and early Kasimovian), an interval of approximately seven million years (Brongniart, 1874, Taylor, 1965; Good et al., 1982, Ogg, 2004). The stratigraphic range of *Trigonocarpus*, which is the compression-impression genus equivalent to *Pachytesta*, may be somewhat longer; nonetheless, *Trigonocarpus* is not known outside the Pennsylvanian (Gastaldo and Matten, 1978).

The distribution of sclerotesta traits among *Pachytesta* species suggests a phylogenetic hypothesis for Taylor's (1965) four groups (Fig. 19). Taylor's first group (*P. shorensis, P. vera, P. muncii, P. sharasperma* and *P. hoskinsii*) is characterized by a sclerotesta composed of interweaving bands of fibers. As discussed above, this trait appears in the earliest known *Pachytesta* species, *P.*

shorensis and *P. olivaeformis*, and appears to be primitive within the genus. For this reason, most members of Taylor's group 1 are shown as an unresolved polytomy reaching to the base of the clade on Figure 19. Because *P. vera* and *P. muncii* share so many characters they are shown as sister taxa; indeed *P. muncii* appears to be a smaller version of *P. vera* (Cichan and Taylor, 1981). Phylogenetic resolution of other species within this group will require additional characters.

Taylor (1965) placed *P. olivaeformis* in group 1. Yet, *P. olivaeformis* has a two part sclerotesta composed of an inner layer of interweaving fibers and an outer layer of radially arrayed fibers that form three tertiary ribs between each pair of primary ribs. Because it possesses many tertiary ribs, I hypothesize that *P. olivaeformis* belongs to Taylor's group 3, the *composita – illinoensis* lineage. *Pachytesta sp. A* and an additional undescribed species from the diverse cordaitean flora of Iowa, *P. sp. B*., also belong in this lineage. *P. olivaeformis, P. composita, P. illinoensis* and *P. sp. A.* all share the trait of having many ribs or ridges. In these four species, secondary ribs and tertiary ribs are difficult to distinguish, especially in the middle of the seed. According to this phylogenetic hypothesis for *Pachytesta* species, the shared derived characters that distinguish Taylor's group 3 are: many ribs or ridges and similar expression of secondary and tertiary ribs in the sclerotesta. *P. sp. B* has only six ribs, three primary and three secondary; however its apical configuration is nearly identical to *P. sp. A*. In addition, both *P. sp. A* and *P. sp. B* have tangential, horizontal fibers in the

innermost layer of the sclerotesta, a trait unique to these two species. Accordingly, I have placed *P. sp. B* in Taylor's group 3.

All species in Taylor's group 4 (*P. stewartii, P. hexangulata, P. berryvillensis, P. pusilla*, and an undescribed species from the diverse cordaitean flora of Iowa, *P. sp. C*) share a two parted sclerotesta with an inner layer of fibers running parallel to the long axis of the ovule and an outer radial 'palisade' layer, which appears to be a derived character for this *Pachytesta* lineage. *P. olivaeformis* has a very similar sclerotesta, the only differences being in *P. olivaeformis*, the inner layers is composed of interweaving fibers and the outer layer of radially elongate fibers varies in length and forms tertiary ribs. Thus Taylor's group 4 may be the 'sister lineage' of the *olivaeformis-composita-illinoensis-sp.A-sp.B* lineage. However, phylogenetic resolution of taxa in these two lineages requires additional traits.

Taylor's group 2, *P. noei, P. gigantea* and *P. incrassata* share an extremely thick sclerotesta, which appears to be a derived trait for *Pachytesta*. Possession of this character suggests that these three species also constitute a separate lineage within *Pachytesta*.

CHAPTER III

CONCLUSIONS

P. sp. A. is a new species of *Pachytesta* from the Late Atokan - earliest Desmoinesian, (ICS Moscovian) of Iowa. It is distinguished by the presence of many low ridges in the sclerotesta, the presence of horizontal fibers in the inner layer of the sclerotesta, and a unique apical configuration. The ridges of *P. sp. A*. appear homologous to the tertiary and secondary ribs of *P. composita* and *P. illinoensis*. Based on the presence of these ridges and similarities to the apical configuration of *P. illinoensis, P. sp. A* appears to belong to the *P. composita - P. illinoensis* group of Taylor (1965).

The diverse cordaitean assemblages of Iowa contain a rich diversity of medullosans. With the addition of *P. sp. A*, all of Taylor's *Pachytesta* groups are represented in this flora: *P. vera* of the *vera-muncii-hoskinii-saharsperma* group; *P. noei* of the *noei-gigantea-incrassata* group; *P. sp. A* of the *olivaeformis-composita-illinoensis* group; and an undescribed species belonging to the *stewartii-pusilla-berryvillensis* group.

There is still a good deal of potential research to be done on the subject of *Pachytesta.* The next logical step to take in this field would be to complete descriptions of the remaining known, undescribed species of *Pachytesta.* A following comprehensive cladistic analysis of all known *Pachytesta* species would further the understanding of the complex evolutionary history of this Genus.

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APPENDIX

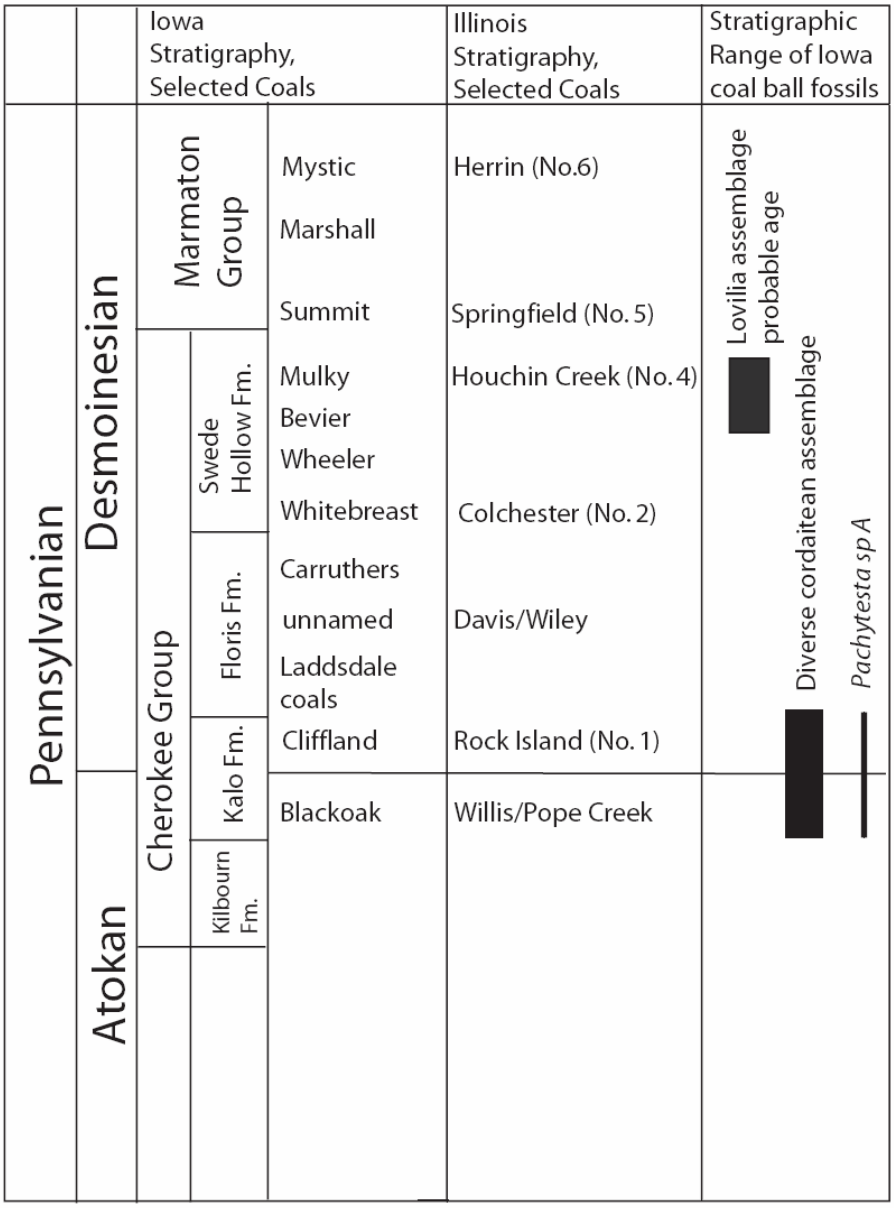

Figure 1: Iowa coal stratigraphy, the age of Brotzman's (1974) Lovila and diverse cordaitean assemblages, and the range of *Pachytesta* sp. A. Stratigraphic correlations from Ravn (1986) and Peppers (1996).

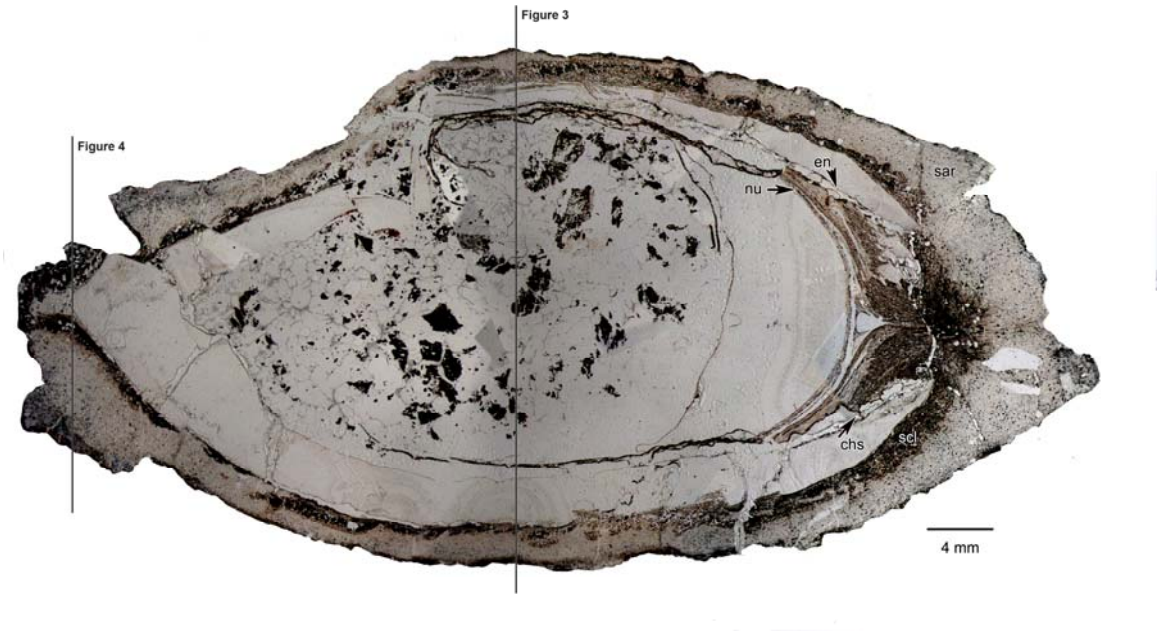

Figure 2: *Pachytesta sp. A*, longitudinal section. Vertical lines indicate the approximate position of Figures 3 and 4. Abbreviations: chs - chalazal skirt; en - endotesta; nu - nucellus; sar - sarcotesta; scl - sclerotesta. HU 64899, ovule E, Urbandale Mine, Polk Co. Iowa. Composite photograph.

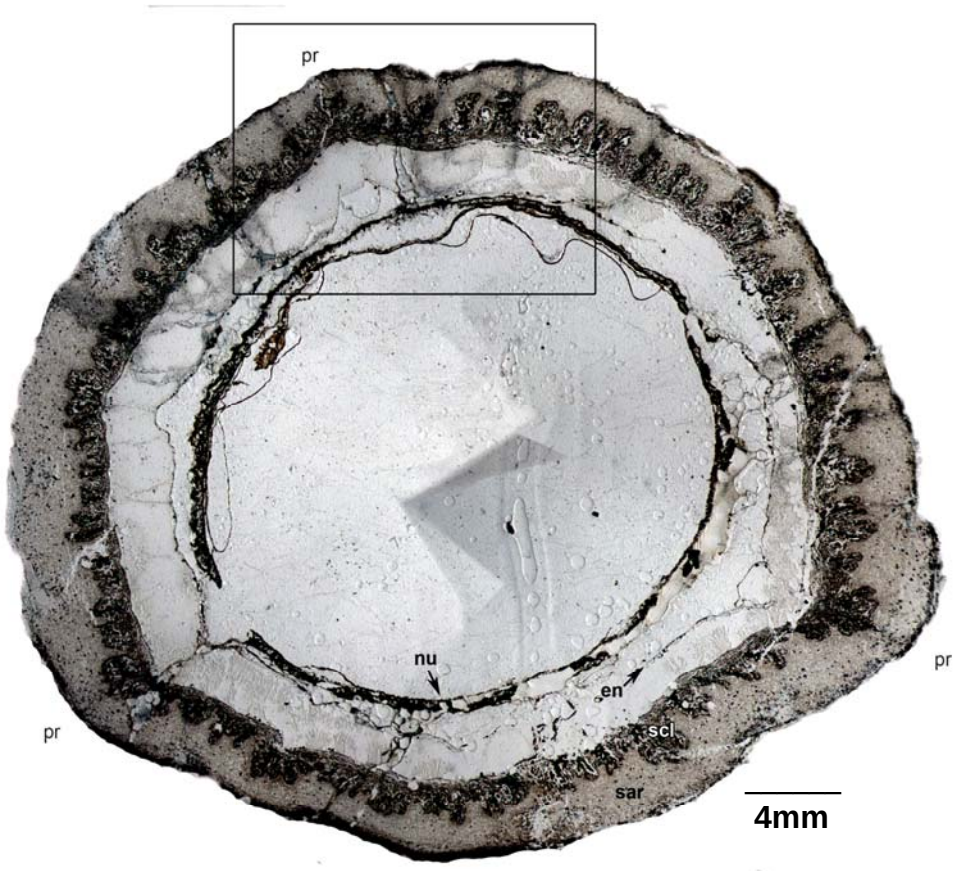

Figure 3: *Pachytesta sp. A*. cross-section in middle of ovule. The rectangle indicates the approximate location of Fig. 4. and Fig. 9. Abbreviations: en - endotesta; nu - nucellus; pr - primary rib; sar - sarcotesta; scl – sclerotesta; pr – primary rib. HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa. Composite photograph.

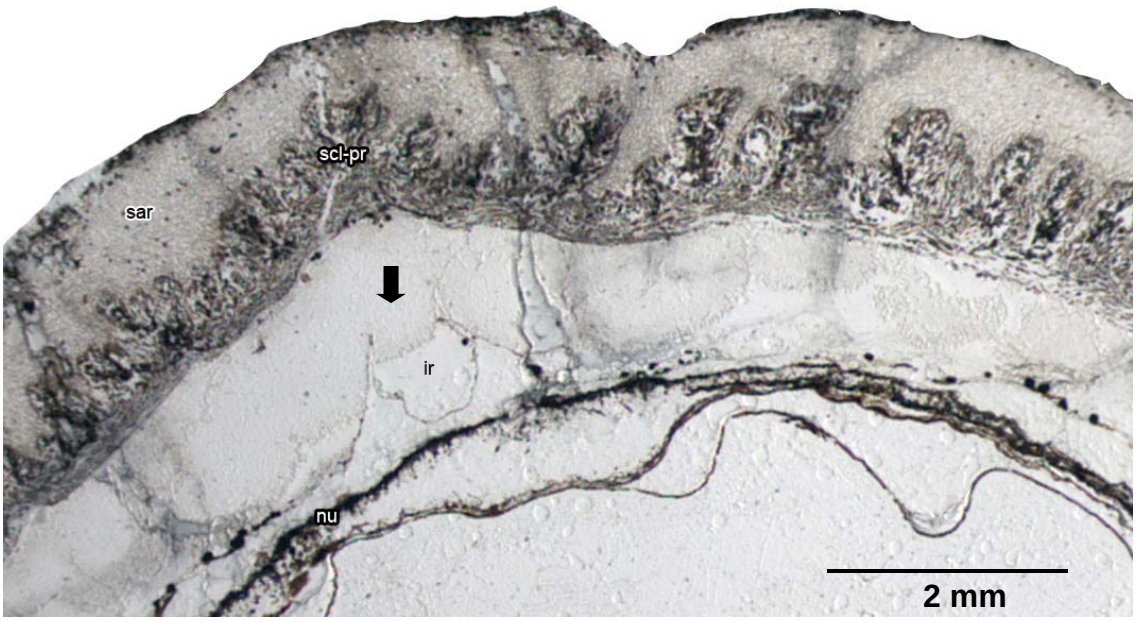

Figure 4: *Pachytesta sp. A*. cross section in middle of ovule. Shows internal rib in the seed cavity adjacent to the primary rib. Short black arrow indicates the location of the internal rib. The black arrow with the shaft indicates the location of the primary rib. Abbreviations: ir - internal rib; nu – nucellus; sar – sarcotesta; scl-pr – sclerotesta at primary rib. HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa.

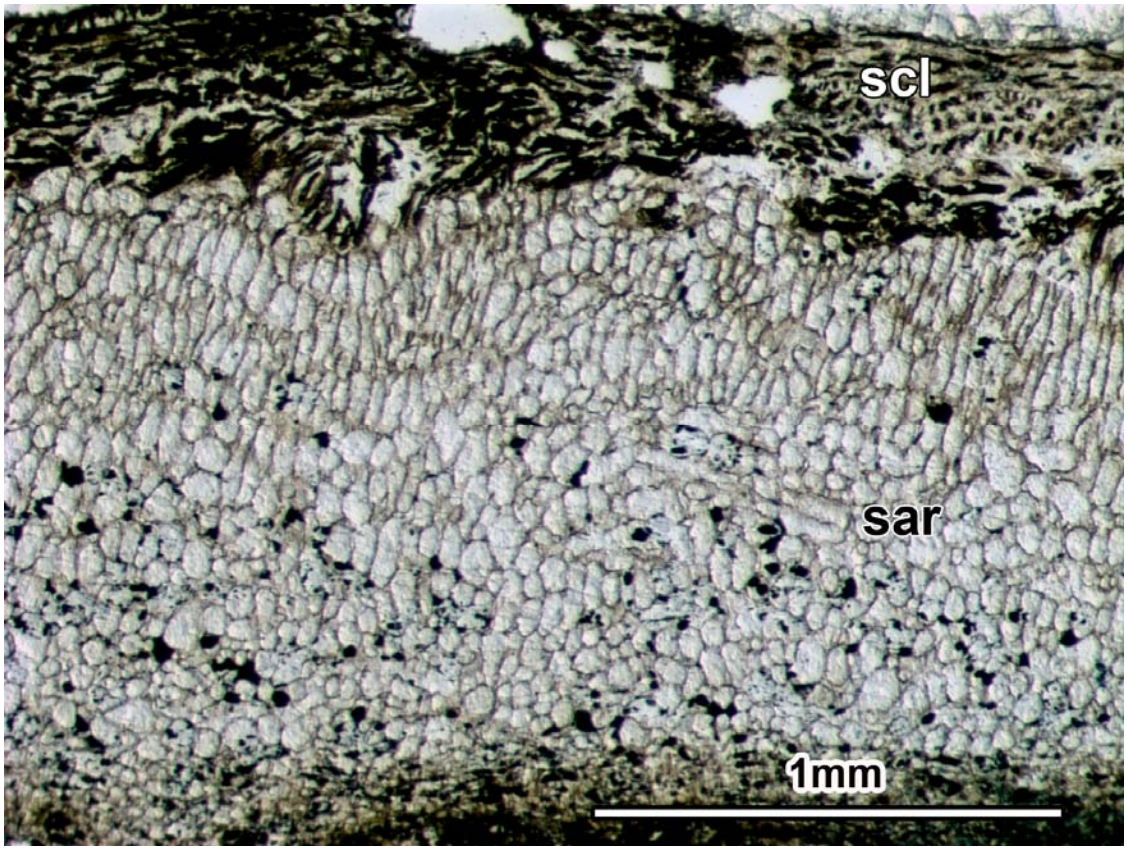

Figure 5: *Pachytesta sp. A,* longitudinal section of integument near middle of ovule. Shows random orientation of parenchyma sarcotesta cells. Abbreviations: sar - sarcotesta; scl - sclerotesta. HU 64899, ovule E, Urbandale Mine, Polk Co. Iowa.

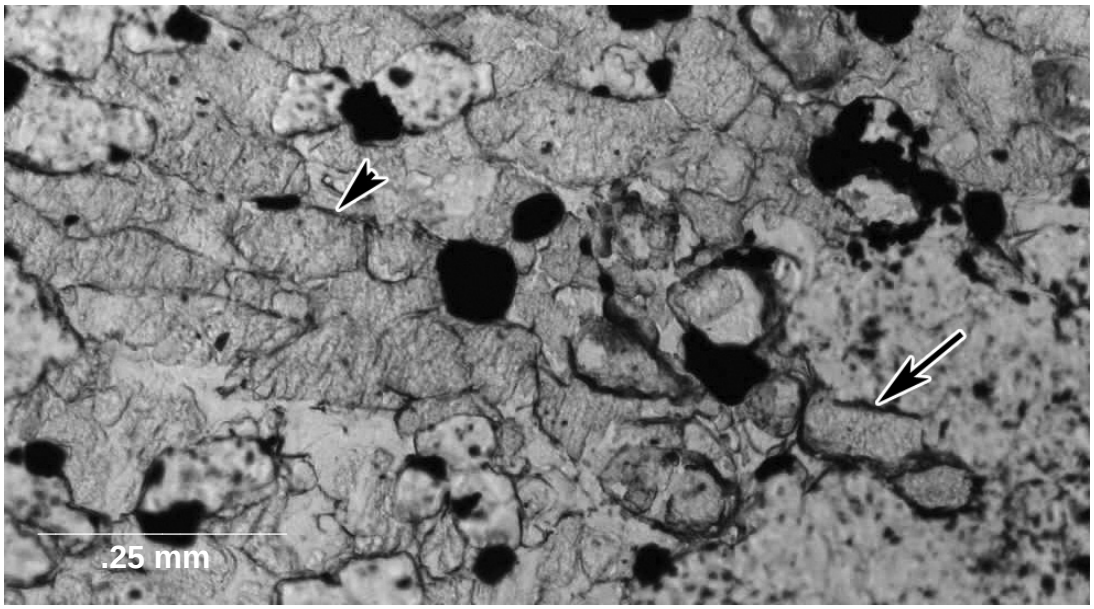

Figure 6: *Pachytesta Sp. A*. cross-section of sarcotesta showing dark walled-cells. These may indicate the position of vascular bundles in the sarcotesta. Arrow with shaft indicates dark walled cells; arrow with no shaft indicates normal parenchyma cells of the sarcotesta. HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa.

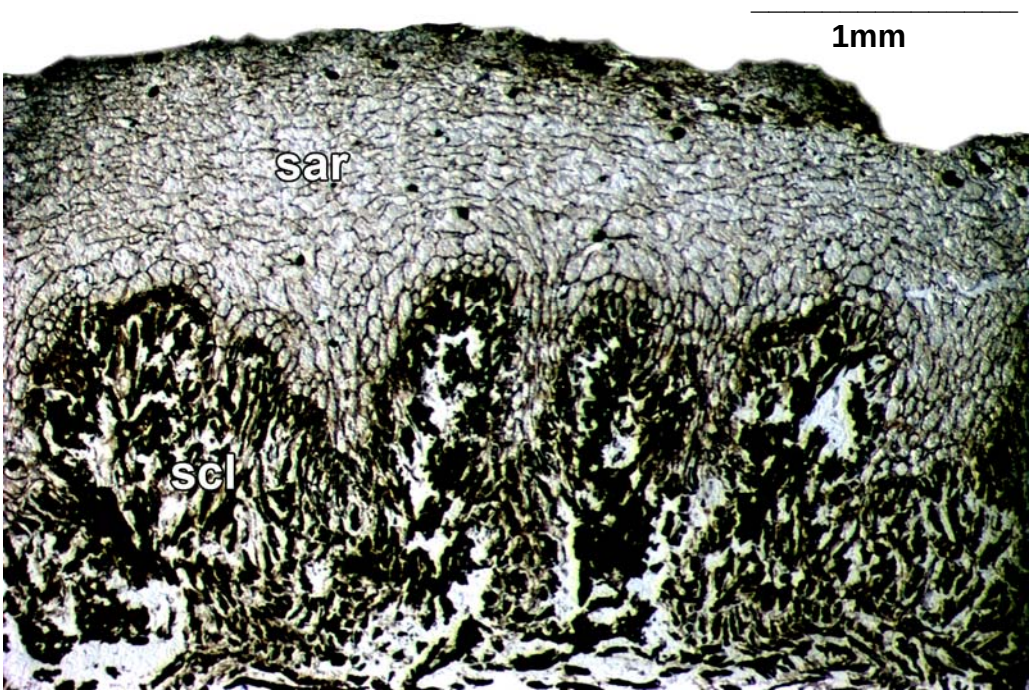

Figure 7: *Pachytesta sp. A*. cross-section of integument in middle of ovule. Shows orientation of sarcotesta cells. Abbreviations: sar – sarcotesta; scl – sclerotesta. HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa.

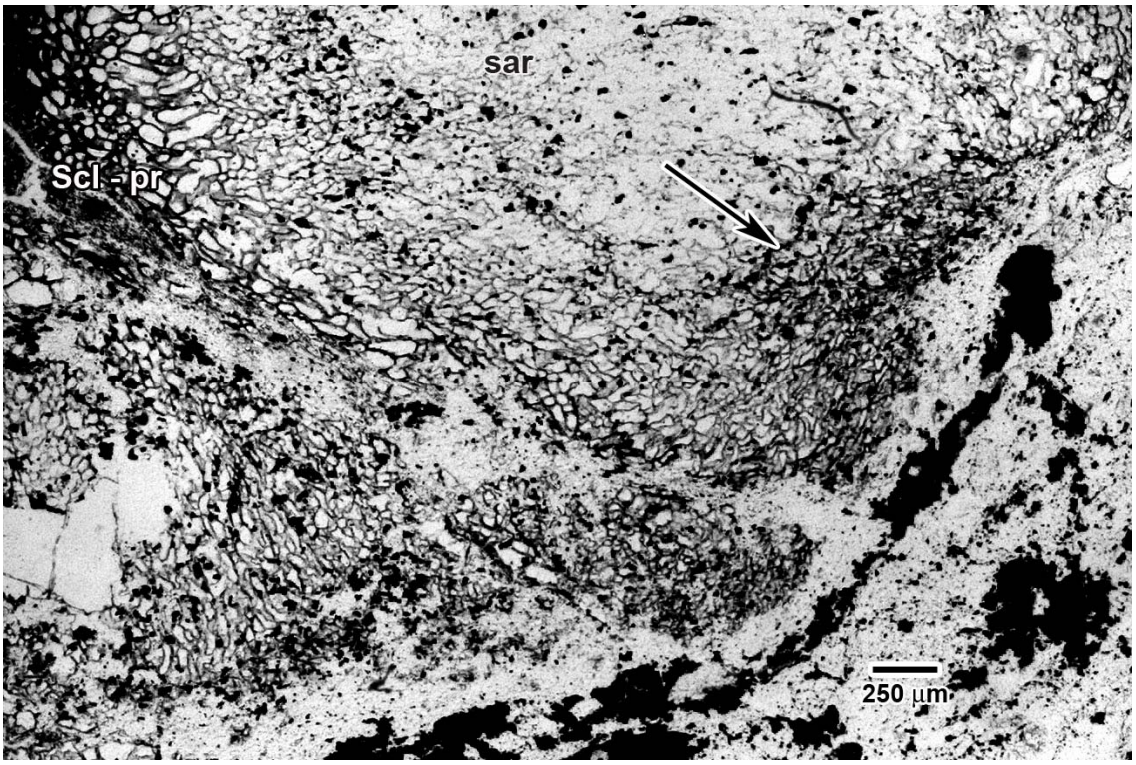

Figure 8: *Pachytesta sp. A*. sarcotesta near the apex. Arrow indicates dark walled cells, showing probable position of vascular bundle in sarcotesta. Abbreviations: sar - sarcotesta; scl-pr - sclerotesta of primary rib. HU 64982, ovule A, Shuler Mine, Dallas Co., Iowa.

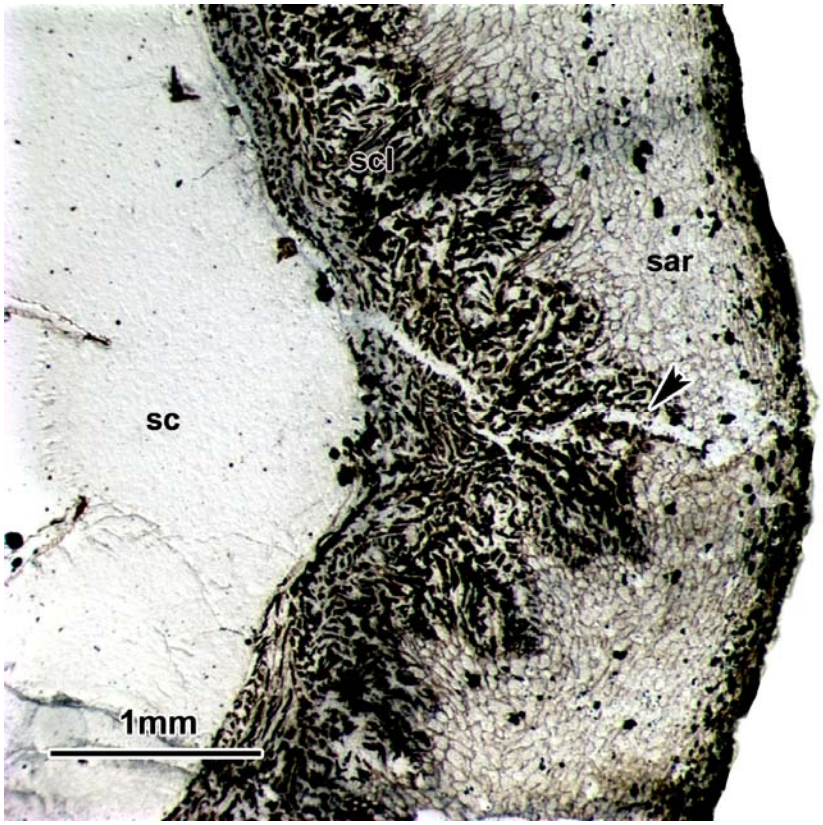

Figure 9: *Pachytesta sp. A*. cross-section of primary rib in middle of ovule. Arrow indicates crack in specimen in the approximate location of the commissure. Abbreviations: sar - sarcotesta; sc - seed cavity; scl - sclerotesta, HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa.

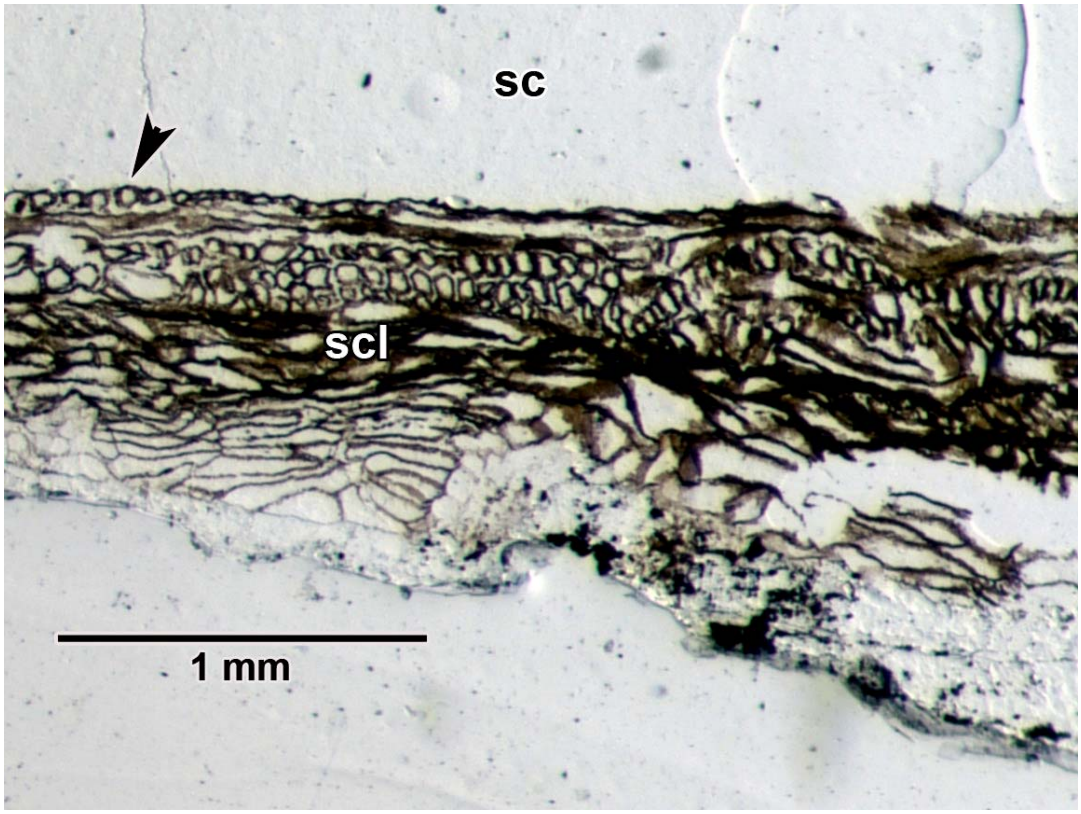

Figure 10: *Pachytesta sp. A*. sclerotesta longitudinal section. Showing orientation of fibers in sclerotesta. Arrow shows the cross-section of fibers wrapping around the seed in a horizontal, tangential direction. Abbreviations: sc - seed cavity; scl - sclerotesta. HU 64983, ovule C, Shuler Mine, Dallas Co., Iowa.

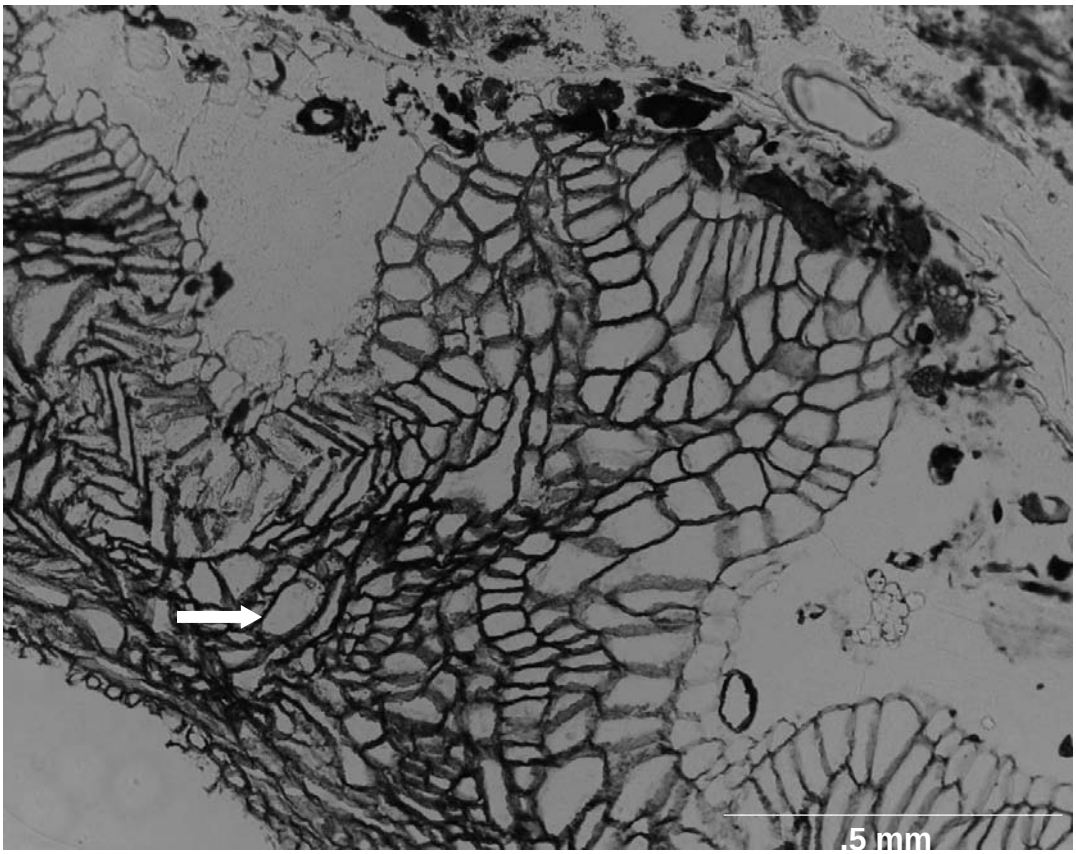

Figure 11: *Pachytesta sp. A*. cross section showing orientation of fibers in sclerotesta. White arrow shows ovoid cell which may be secretory. White arrow indicates fibers oriented parallel to the longitudinal axis of the seed. HU 64983, ovule C, Shuler Mine, Dallas Co., Iowa.

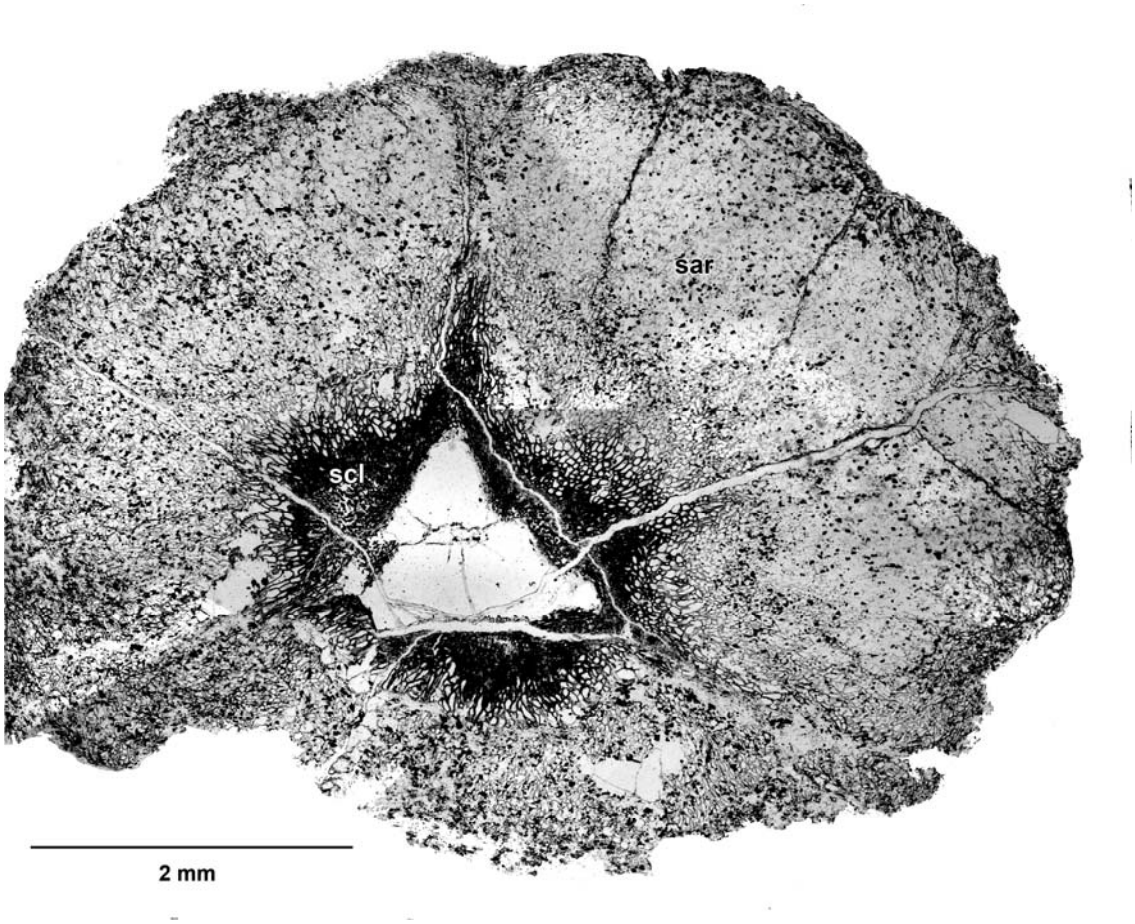

Figure 12: *Pachytesta sp. A*. sarcotesta near the apex. Arrows show regions with broken parenchyma cell walls which may indicate the development of a lacunate sarcotesta. HU 64982, ovule A, Shuler Mine, Dallas Co., Iowa.

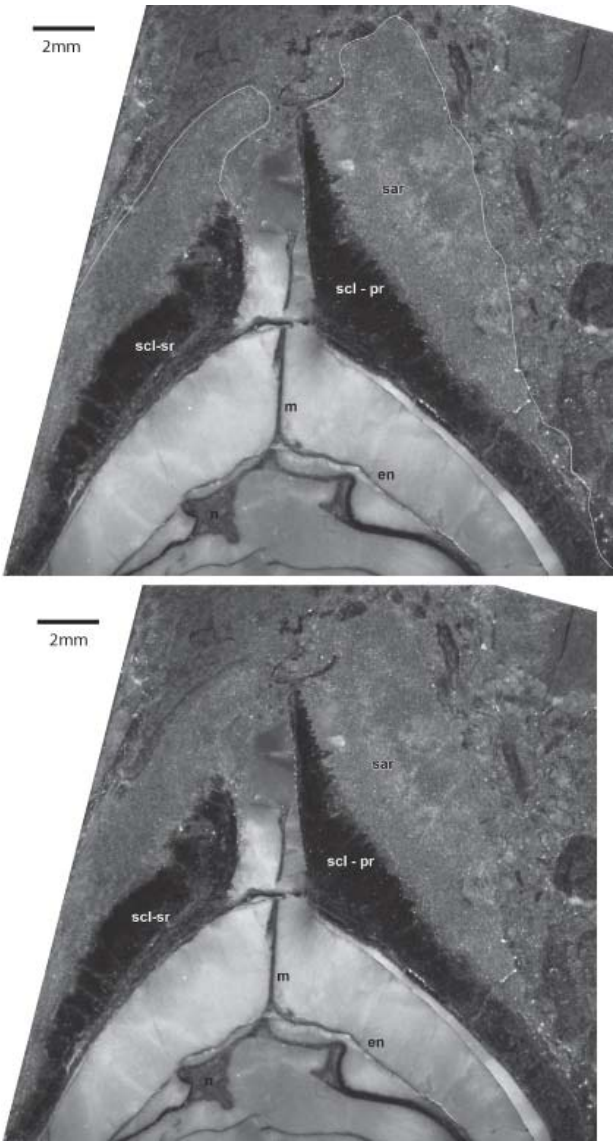

Figure 13: *Pachytesta sp. A*. longitudinal section of apex. This figure represents a composite of the part with a mirror image of the seed cavity of the counterpart superimposed, in order to show the complete length of the micropyle in one image. The micropyle is missing at the top of the seed cavity due to removal by the saw when making this cut. In upper figure, the white line indicates the outer edge of the sarcotesta. The micropyle is an extension of the endotesta, surrounded by a collar of sclerotesta and sarcotesta. Abbreviations: en - endotesta; m - micropyle; n - nucellus; sar - sarcotesta; scl-pr - sclerotesta of primary rib; scl-sr - sclerotesta of secondary rib. HU 64982, ovule B, Shuler Mine, Dallas Co., Iowa. Composite photograph.

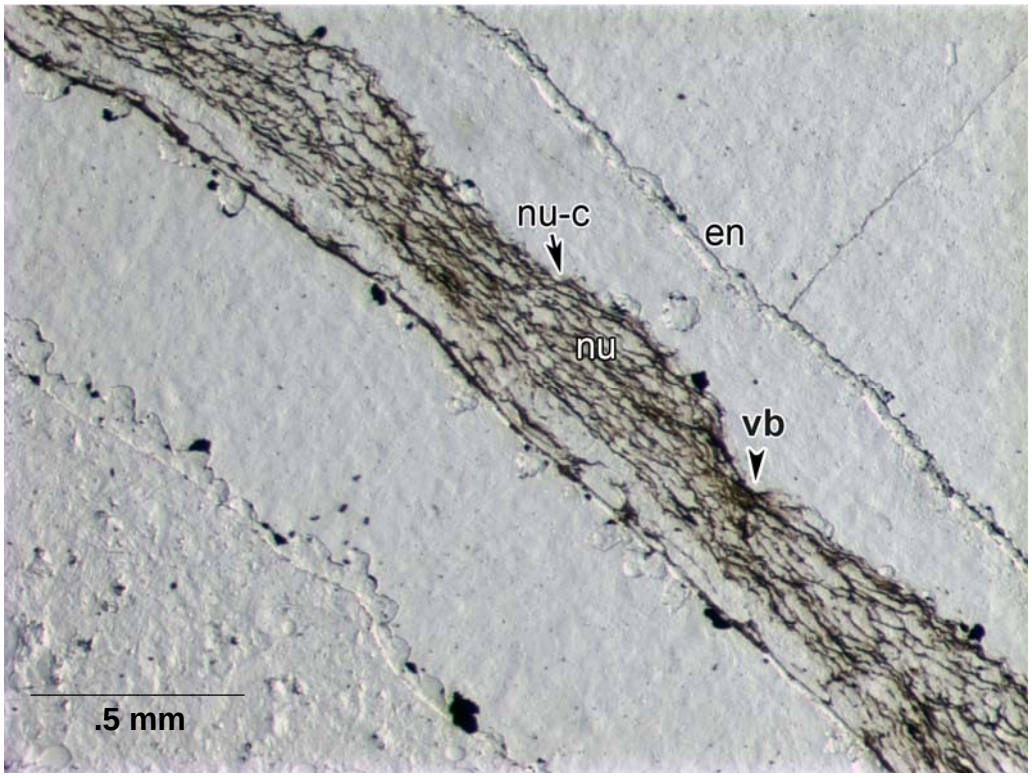

Figure 14: ***Pachytesta sp. A*****. cross section in middle of ovule showing the cuticule of the nucellus and endotesta. The arrow labelled nu-c indicates the cuticle of the nucellus, which has an undulating surface. The cuticle of endotesta reflects the circular outline of the seed cavity defined by the sclerotesta. The arrow labelled vb indicates the position of the vascular bundle. HU 64982, ovule B, Shuler Mine, Dallas Co., Iowa.**

Figure 15: Apical reconstruction of *Pachytesta sp. A* based on Ovule B

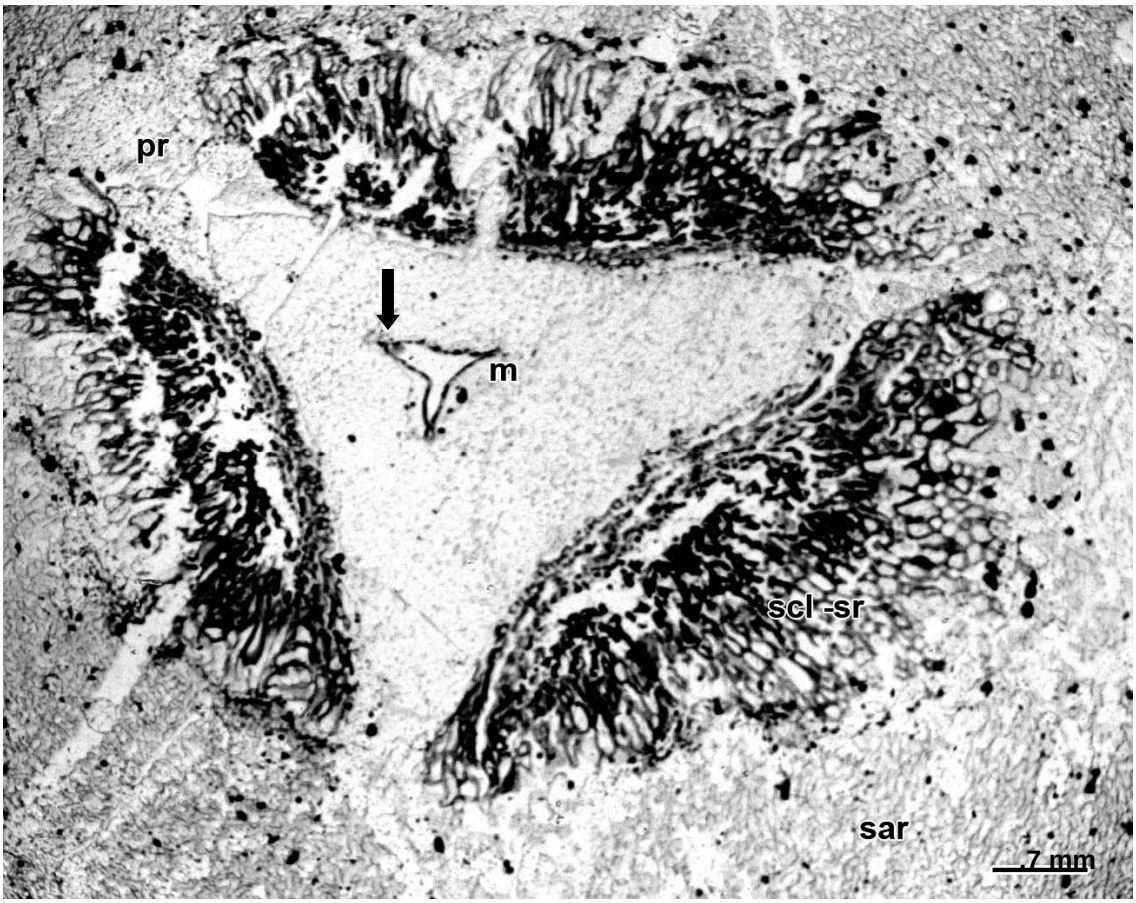

Figure 16: ***Pachytesta sp. A*** **cross-section near the apex showing the triangular cross-section of the micropyle. Black arrow indicates pollen grain location. Abbreviations: m - micropyle; pr - primary rib; sar - sarcotesta; scl-sr - sclerotesta of secondary rib. HU 64899, ovule D, Urbandale Mine, Polk Co., Iowa.**

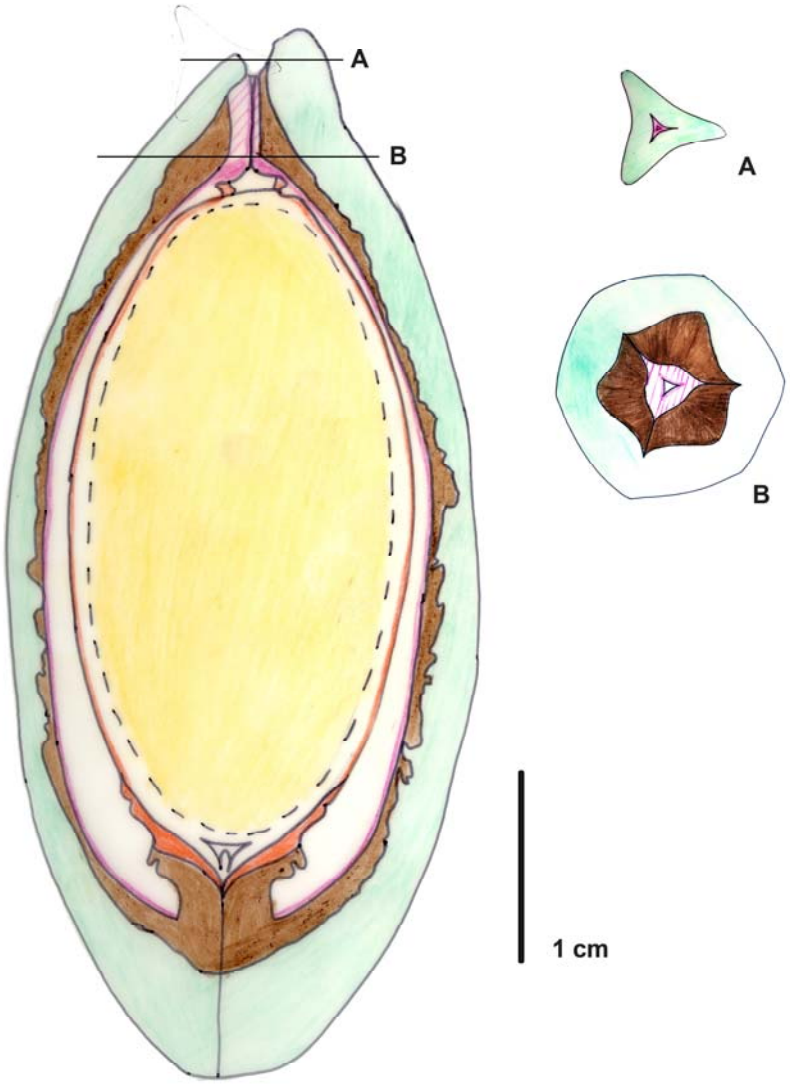

Figure 17: Reconstructed longitudinal section and apical cross sections of *Pachytesta sp. A.* Key to colors: Sarcotesta - green; sclerotesta - brown; endotesta - magenta; nucellus - orange; megaspore - yellow. The megaspore membrane is dashed. The micropyle is triangular in cross section and is formed from endotesta. The sclerotesta and sarcotesta form a 'neck' for the micropyle. The magenta stripes indicate possible presence of endotesta cells filling the space between the sclerotesta and the micropyle .

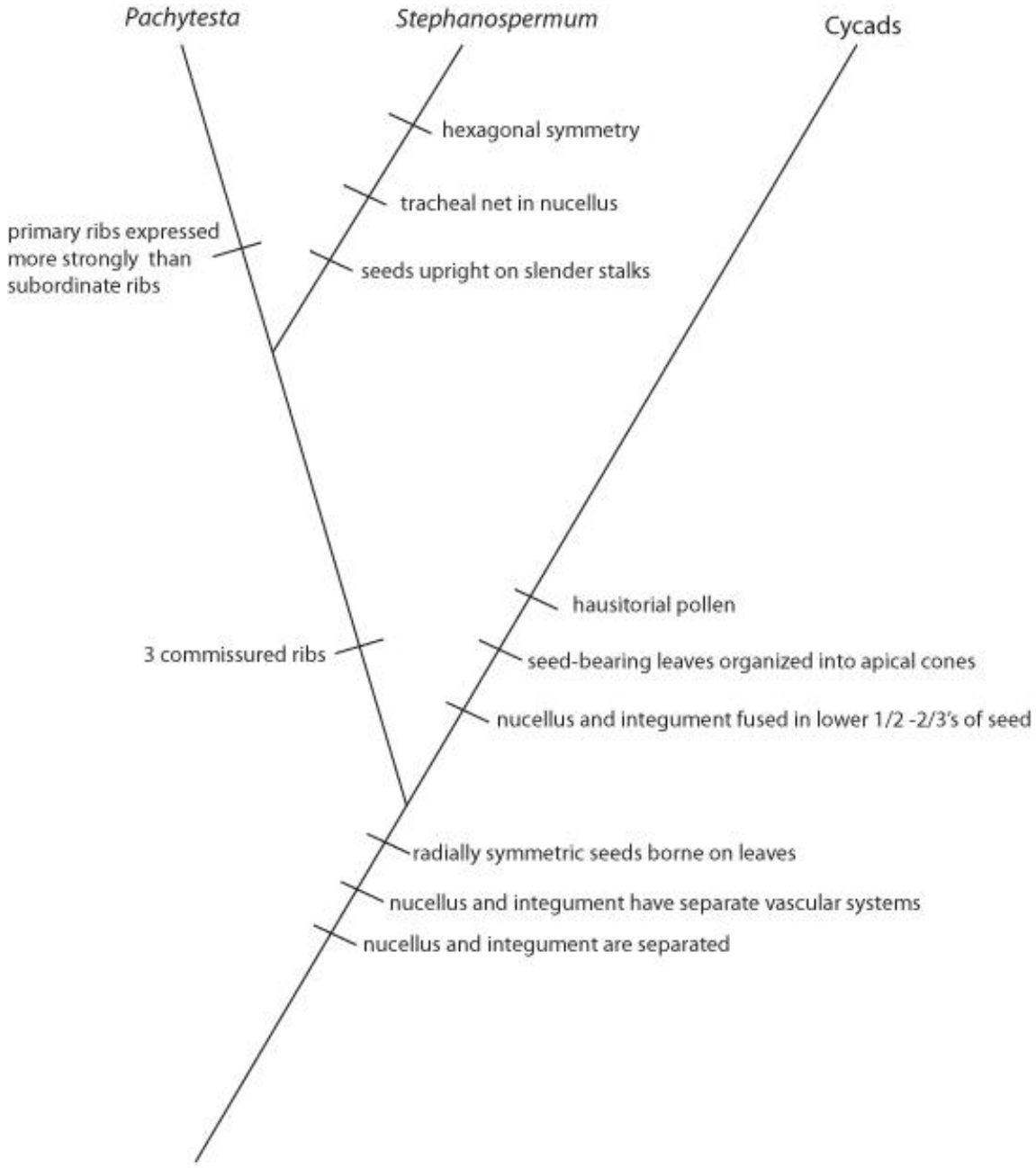

Figure 18: Cladogram. Shows the relationship between cycads and the medullosan seeds, *Pachytesta* and *Stephanospermum* based on seed characters.

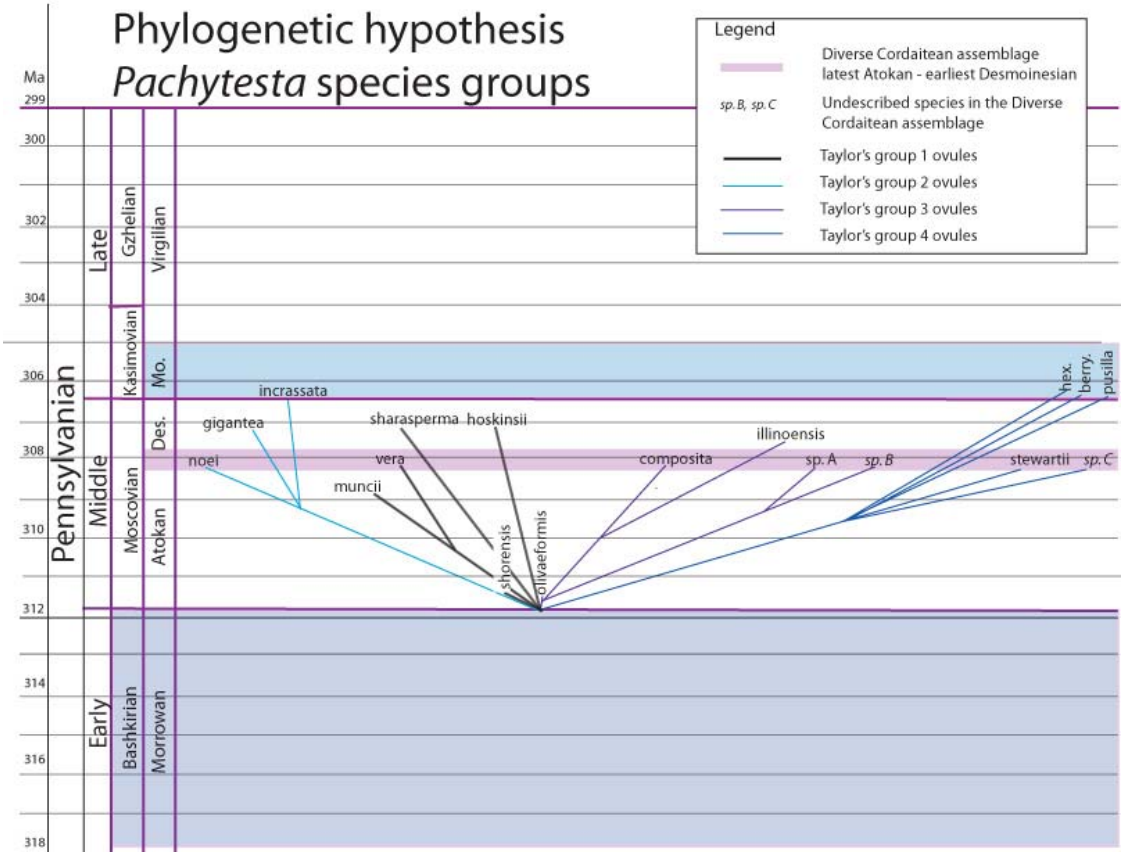

Figure 19: *Pachytesta* Cladogram. Shows possible relationships among the four *Pachytesta* groups of Taylor (1965) based primarily on characters found in the slcerotesta. *Pachytesta sp. A*. probably forms a lineage with *P. composita* and *P. illinoensis*; *P. olivaeformis* may belong to this lineage as well. Species in Taylor's group 1 share a sclerotesta formed of interweaving bands of fibers, which appears to be a primitive character of *Pachytesta*.

VITA

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